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Shell size and growth rate differences for alpine populations of *Arianta arbustorum* (L.) (Pulmonata : Helicidae)

by

Bruno BAUR *

With 2 figures

Abstract

Since in the Alps adult size of *Arianta arbustorum* (L.) tends to decrease with the altitude of the site, snails from high and low altitude were reared from egg to adulthood in the laboratory under identical conditions. The eggs were laid by snails that had been sampled from two mountain sites and the corresponding foot of the slopes. During ontogeny the shell diameter was measured weekly.

Laboratory-reared snails from valley populations grew to the same size as snails from nature at the same sites, whereas laboratory-reared snails from mountain populations grew larger than their field counterparts. In the laboratory, *A. arbustorum* from mountain populations required more time to accomplish growth and had a smaller juvenile growth rate than snails from corresponding valley populations. Juvenile growth rate is positively correlated with adult shell diameter. Snails from valley populations lay larger eggs than snails from the mountains.

INTRODUCTION

On mountain slopes in the Alps, the landsnail *Arianta arbustorum* (L.) tends to be small (Bütikofer 1920; Favre 1927; Wolf 1933/34; Burla & Stahel (in press)) while at low altitude larger snails are found. Variation in shell size has been considered in

* Zoological Museum, University of Zurich-Irchel, Winterthurerstr. 190, CH-8057 Zurich, Switzerland.

other snails as well, such as *Cepaea nemoralis* (L.) and *C. hortensis* (Müller), and attributed to various causes. In *C. nemoralis* it may be related to topography (Cameron & Cook 1971), geographical position (*C. hortensis* by Häkkinen & Koponen 1982), predation (Bantock & Bayley 1973) and population density (Williamson *et al.* 1976; Cameron & Carter 1979; Cook & Cain 1980). However, variation in shell size has been observed over short distances even in uniform habitats by Wolda (1969).

This study attempts to find out whether size differences between mountain- and valley-dwelling *A. arbustorum* persist in snails reared under standard laboratory conditions. If such variation is maintained, a genetic component is implied in the determination of shell size.

MATERIAL AND METHODS

Adult snails were collected in June 1978 in two areas, Davos and Scuol, in the eastern Swiss Alps. The distance between the two areas is about 40 km. In the Davos area, the mountain sample came from the south-facing slope of the Schiahorn, 2400 m above sea level, and the valley sample from a railway escarpment in Dalfazza near Klosters at 800 m. In the Scuol area, the mountain sample came from Alp Clünas at 2500 m and the valley sample from the delta of the river Clozza at 1200 m. Each sample was obtained within a circle of 20 m diameter.

These snails were allowed to lay eggs in the laboratory. From each sample eight clutches were separated and after hatching forty juvenile snails of each population were picked out at random and individually marked with numbers in Indian ink. Each group of snails was split into two batches of twenty and put into transparent, oblong plastic containers measuring 20 × 10 × 7,5 cm. The bottoms of these containers were covered with soil mixed with powdered lime. The room temperature was 18° ± 2° C. The animals were fed on lettuce.

The diameter of the shell (d) of each snail was measured weekly to the nearest 0.1 mm as described by Wolda (1963). d^3 is closely related to snail weight (Williamson 1976; Andreassen 1981). When the average shell diameter in any breeding container reached 7 mm, the snails were placed in a larger container measuring 33 × 22 × 9 cm. Measurements were continued until growth was completed with the formation of a lip. Some of the snails died, e.g. in the Scuol mountain group only 15 snails reached adulthood.

The marking and weekly measuring did not influence shell size. Snails kept under the same conditions, but unmarked and only measured when adult, showed no significant difference in shell size when compared with snails which were measured weekly (Mann-Whitney *U*-test, $p > 0.10$).

Additional data about egg-size came from populations near Elm at 1300 m and Zurich at 600 m. The maximum diameters of the nearly spherical eggs were measured under a binocular microscope using a stage micrometer.

RESULTS

Table 1 shows the mean shell diameter of the parent snails, the laboratory raised snails (F1) and additional field samples (from Burla & Stahel, in press). Figure 1 shows the distributions of shell size. Valley and mountain field samples from both Davos and Scuol differ significantly (Mann-Whitney *U*-test, $p < 0.001$ resp. $p < 0.01$). This

TABLE 1.

Shell diameter of *A. arbustorum*. All measurements are given in millimeters.
N = sample size, S.D. = standard deviation.

Area	Group	Field sample				Parents				Laboratory group (F1)			
		Mean	S.D.	Range	N	Mean	S.D.	Range	N	Mean	S.D.	Range	N
Davos	Mountain	13.5	0.6	12.1-14.5	25	13.5	0.6	12.3-14.3	25	16.1	0.8	14.7-18.1	28
	Valley	19.4	1.2	17.6-21.8	10	19.9	1.3	18.5-21.9	7	19.1	0.8	17.5-20.4	23
Scuol	Mountain	17.3	0.7	15.6-18.8	25	17.0	0.7	16.2-18.9	13	18.4	0.9	16.7-19.6	15
	Valley	19.3	0.8	18.0-21.0	25	19.6	1.3	17.8-22.6	16	19.5	1.2	17.5-21.2	33

difference is less in laboratory-reared snails, but remains significant (Mann-Whitney *U*-test, Davos area $p < 0.01$, Scuol area $p < 0.05$). Under laboratory conditions, snails from the valley (both localities) grew to be as large as those of the parent field populations,

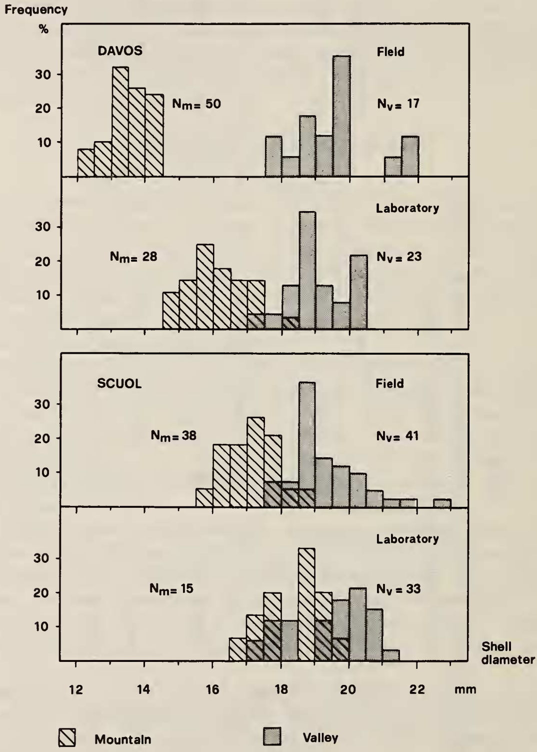

FIG. 1.

Distribution of the shell diameters of *A. arbustorum*.
N_m = number of mountain snails, N_v = number of valley snails.

whereas the laboratory-reared mountain snails became significantly larger than their progenitors (Mann-Whitney *U*-test, Davos area $p < 0.001$, Scuol area $p < 0.01$). The differences in mean shell diameters between mountain and valley snails are about half as large in the laboratory groups as in the field samples (Table 1). The regression of mean diameter of offspring on mid-parent size has a slope of 0.54, which estimates heritability (FALCONER 1960).

TABLE 2.

Period of growth in *A. arbustorum* under laboratory conditions, in days. N = number of snails.

Area	Group	Growth period		N
		Mean	S.D.	
Davos	Mountain	185	24	28
	Valley	173	13	23
Scuol	Mountain	186	14	15
	Valley	174	17	33

TABLE 3.

Specific growth rate in *A. arbustorum* under laboratory conditions, in days $^{-1}$, during the first 120 days after hatching from the egg.

Area	Group	Specific growth rate		Number of snails
		Mean	S.D.	
Davos	Mountain	0.0114	0.008	28
	Valley	0.0134	0.009	23
Scuol	Mountain	0.0145	0.008	15
	Valley	0.0147	0.011	33

Duration of growth (time from hatching to lip production) was significantly greater in both mountain groups than in the corresponding valley groups (Mann-Whitney *U*-test, both areas $p < 0.05$). The mean values are shown in table 2. The shortest duration of growth was 137 days (a snail of the Scuol valley group), and the longest 234 days (an individual from the Davos mountain group).

The growth curves obtaines from weekly measurements of shell diameter are shown in figure 2. All growth rates were approximately exponential in the first 120 days, which permit us to establish an exponential curve and to compare relevant parameters (table 3).

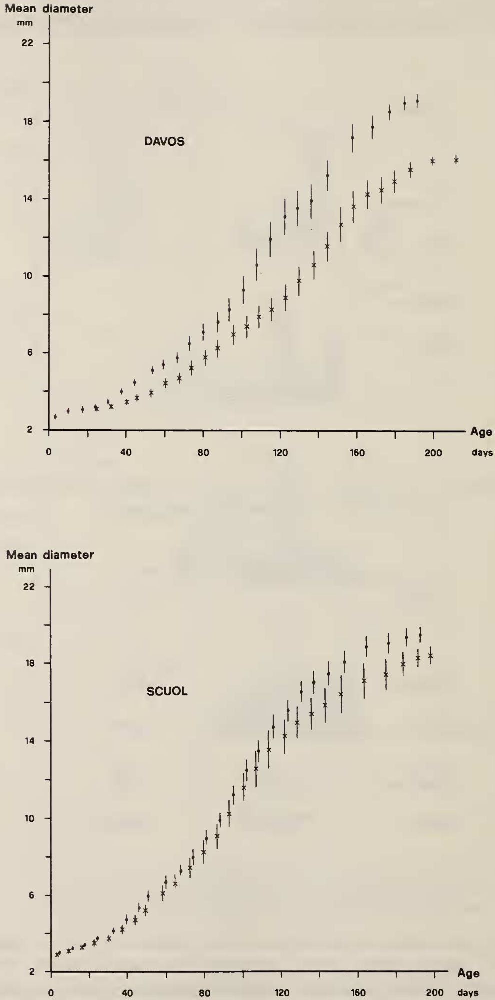

FIG. 2.

Growth curves in *A. arbustorum* under laboratory conditions, mean with 95 per cent confidence limits (x = mountain sample, • = valley sample).

TABLE 4.

Egg diameter and clutch size of *A. arbustorum.*

Area	Altitude (m above sealevel)	Egg diameter (mm)		Clutch size			Sample size
		Mean	S.D.	Mean	S.D.	Range	
Davos	2400	2.4	0.1	19	7	11-25	3
Elm	1300	3.1	0.1	29	9	19-51	9
Zurich	600	3.3	0.1	51	13	39-69	4

The Davos mountain offspring had a smaller specific growth rate in the first 120 days than the corresponding valley snails (Mann-Whitney *U*-test, $p < 0.01$). Also the Scuol mountain offspring had a smaller specific growth rate than the valley snails, but there the difference is not significant. When the data from all four groups are combined, the correlation between the specific growth rate of the juveniles and the shell diameters of the adults is highly significant ($r_s = 0.73$, $p < 0.001$, Spearman rank correlation).

Table 4 shows egg diameter and clutch size from various populations. Both egg size and clutch size seem to decrease with increasing altitude.

DISCUSSION

When snails are bred from different sites under standard laboratory conditions there are differences in physiological acclimatization. But the size of individuals from different populations grown up under the same conditions may also vary, possibly due to differences in genetic constitution. The range of size within populations is usually quite small, but differences between populations from very dissimilar environments may be large.

The adult shell diameter of *A. arbustorum* from high and low altitudes differ also under identical breeding conditions. This indicates that a genetic component is implied in the determination of shell size. The measurement of heritability depends on the specific environmental conditions on which the breeding is done. The heritability does not tell whether any given trait is produced by a deterministic biochemical pathway during development. In *C. nemoralis* the heritability of shell size is about 0.60 (COOK 1967; WOLDA 1969), in *A. arbustorum* 0.70 (COOK 1965; COOK & KING 1966). The latter may be an overestimate due to the use of parents from different populations with very different shell sizes (JONES *et al.* 1977) and evidence from natural populations indicates that the environmental effect on size may be greater than it is suggested by these estimates (COOK & O'DONALD 1971; COOK & CAIN 1980). It is clear from the present experiment that the place of origin affects the response in shell size.

In *Cepaea* various environmental factors may influence size, e.g. temperature, humidity, light intensity, calcium availability (OOSTERHOFF 1977) and population density

(Williamson *et al.* 1976). During the winter, when the snails are dormant, selective mortality could change mean size in a population, as suggested by the experimental results of Cook & O'Donald (1971) for *C. nemoralis*.

What are the advantages of being small or large? Size has a considerable effect on the heat balance of pulmonates: Smaller *C. nemoralis* shells absorb less incident radiation and lose heat faster than larger shells (Heath 1976). Knights (1979) found that *C. hortensis* of smaller size was favoured in unshaded conditions and that larger ones survived better in shade. Cook & O'Donald (1971) suggested that cooler conditions in hibernation experiments favoured larger shell size in *C. nemoralis*, while Bengtson *et al.* (1979) seem to suggest the opposite effect in *C. hortensis* in Iceland: During relatively warm winters large snails are at a selective advantage and during colder winters smaller individuals have an advantage. Large size attracts greater predation (Cook & O'Donald 1971; Bantock & Bayley 1973), although juvenile snails are more vulnerable. In cold regions, size is kept small for various biochemical and metabolical reasons in *A. arbustorum* (Gromadska & Przybylska 1960).

In the Alps there are considerable differences in local climate between high and low altitude. The length of the growing season is probably inversely associated with altitude. Snails in the valley are better sheltered from wind and receive little solar radiation during the day. Above the tree-line the snails are more exposed to intense radiation (the ground temperature at 2500 m altitude can reach 60° C and more on a south-facing slope (Turner 1958; Geiger 1965; Franz 1979)). Another problem that a mountain-dwelling snail has to face is the low predictability of the environment. In July, freshly fallen snow occurred on average on 3.8 days at the top of the Säntis (2504 m above sea level) in the past two decades, and ground frosts can be recorded in every month of the year (Schüepp *et al.* 1980). The manner in which these snails adjust to such apparently extreme conditions may be explained by adaptations in behaviour, size and colour.

Snails on mountains have a shorter growth season than the snails in the valleys. Mountain snails grow more slowly and take longer to reach maturity. In nature, newly hatched *A. arbustorum* takes about two years to become adult at an altitude of 600 m in Switzerland (Baur, unpubl.). In populations on mountains however, this time is perhaps insufficient for full growth. In Scandinavia *A. arbustorum* needs three to four years to complete growth (Terhivuo 1978; Andreassen 1981).

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Zusammenfassung

Bei *Arianta arbustorum* in den Alpen nimmt die Schalengrösse der Adulten mit zunehmender Meereshöhe ab. Um zu überprüfen, ob diese Unterschiede erblich sind, wurden Schnecken, deren Eltern aus je zwei Berg- und Talpopulationen stammen, im Labor unter identischen Bedingungen ab Ei aufgezogen. Während der Ontogenese wurde der Schalendurchmesser wöchentlich gemessen.

Die im Labor aufgezogenen Schnecken aus Talpopulationen erreichten die gleiche Grösse wie Tiere, die an den Herkunftsstellen frei aufgewachsen waren, während im

Labor die Schnecken aus Bergpopulationen grösser wurden als die entsprechenden Wildtiere. Tiere aus Bergpopulationen haben im Labor eine kleinere Wachstumsrate und benötigen mehr Zeit, um das Schalenwachstum abzuschliessen als Tiere aus Talpopulationen. Zwischen der Wachstumsrate bei Juvenilen und dem Schalendurchmesser bei Adulten besteht eine enge Korrelation. Schnecken aus Bergpopulationen legen kleinere Eier als Schnecken aus Talpopulationen.

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